THIS REMARKABLE KENTUCKY BLUEGRASS

By Robert W. Schery
The Lawn Institute, Marysville, Ohio

Bob Woodson had a particular "pet," butterfly weed, *Asclepis tuberosa*, on which he lavished many years in study of its populations. So, for this commemorative issue, it is perhaps relevant for me to muse about a lawnsman's "pet," Kentucky bluegrass *(Poa pratensis)*, certainly no stranger to the pages of the Annals (viz. 2, 5). Because bluegrass is one of the outstanding lawngrasses, I have had occasion in recent years to watch its performance rather closely, hoping to relate its population dynamics to the new ecology of suburbia.

Considering *Poa pratensis* to embrace wide-ranging populations found in all states of the U.S.A. (fide Hitchcock, 1), here is a truly remarkable taxon, and one considerably more complex than butterfly weed. European taxonomists have tended to split *Poa pratensis*, but broadly considered the species is ubiquitously circumboreal.

There has long been interest in the exceedingly complicated heredity of Kentucky bluegrass, largely apomictic and highly polyploid. Cytogenetic studies were made by Brown about 1941 (2). Very extensive work was done in Wisconsin from the mid 1930's through the early 1950's, chiefly by E. L. Nielsen and D. C. Smith (3). These and other works show how involved is *Poa pratensis*, even to uncertainty about its diploid chromosome number (a base number of 7 seems to hold, but published chromosome counts reach 147 and higher). Perhaps Barnard (4), discussing grass cytogenetics, summarizes as well as possible: "*P. pratensis* has demonstrated its ability to absorb genomes from many different sources and occasionally give rise to valuable new apomictic segregates. This may explain the polymorphism characteristic of this apomictic complex, and account for its adaptability, and wide distribution throughout the Northern Hemisphere."

With Kentucky bluegrass already so widely treated in the literature, one might suppose that there is relatively little novel to report about it. Nonetheless, most publications have dealt with its physiologic responses or genetic pecularities, or, among agriculturists, with yields and management. One of the relatively few attempts to examine Kentucky bluegrass holistically is that of Etter (5).

It is not my purpose to review the literature on Kentucky bluegrass, which would be a volume unto itself. Rather I will record certain observations made on "wild" (volunteer) stands of "natural" (unselected) *Poa pratensis*, at numerous locations through the Midwest (Kentucky; Missouri-Iowa; Minnesota-Dakotas), over a period of several years. Until very recently most of the Kentucky bluegrass lawn seed was harvested from such stands. Therefore, whether distinctive ecotypes had evolved was of some importance, lest they be only locally or narrowly adapted.

The Lawn Institute, in checking this out, arranged for numerous known-origin seed samples to be planted side by side in various parts of the country. The tests

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Table 1. Sods forced greenhouse. Figures in parenthesis indicate range of variability. Units of measurement are 1/32nds of inch.

	number "clones"	*shoots/ linear 2"*	*mean width 2nd panicle lf.*	*"clone" extremes*	*number samples*	*mean width all vegetative leaves*	*"clone" extremes*	*number samples*
Minnesota	36	6.36 (8-5)	3.21 (4-2)	2.5-3.8	81	2.91 (4-2)	2.5-3.3	360
North Dakota	30	6.37 (8-5)	3.08 (4½-2)	2.5-3.6	86	2.87 (4-2)	2.3-3.6	300
South Dakota	42	6.50 (7-5)	3.31 (4½-2)	2.8-4.0	283	2.94 (4-2)	2.6-3.4	420
Iowa	42		3.53 (5-2)	2.6-4.7	258	3.31 (5½-1½)	2.3-4.8	420
Missouri	44		3.37 (6-1½)	2.0-4.3	154	3.27 (5½-2)	2.4-4.8	450
Kentucky	20	7.45 (9-5)	3.50 (7½-2)	2.6-5.8	75	3.21 (5-2)	2.4-4.5	200

Table 2. Mean leaf width of sods of Table 1, 3 months after planting out, mowed 3". Figures based on 200 measurements. Mowed regularly at 3 inches.

Source	*at April planting*	*July (after 3 mo.)*
Minn.-Dakotas	2.91	2.91
Iowa-Missouri	3.29	3.05

proved rather conclusively that seed harvested in any area, when adequately started in another, gave performance comparable to other sources, including local ones.[1] Occasional immediate differences, such as in rapidity of germination or seedling vigor, are largely non-genetic (but of mechanical or environmental derivation), and vary from lot to lot. Seed lot quality is much influenced by harvesting and processing, and even by the weather (comparing one year with another). Certainly heavier fractions of seed, properly cured and stored, provide better germination and greater seedling vigor, hence often a better stand. Thus, although one can presume local ecotypes (as from high vs. low ground), there is great adaptability in the mixed population (bag of seed containing all such ecotypes) as it comes to market.

More surprising than wide adaptability is natural bluegrass' unusual flexibility, such that it may change morphologically with the habitat. In as little as three months, sods from widely divergent habitats, presumably representing such distinctive ecotypes as were there, molded towards a norm when planted side by side on our test grounds. Ahlgren, Smith & Nielsen (6) pointed out years ago, with bluegrass "grown in small plots there is a marked tendency for original differences between most strains to become less pronounced as seedings increased in age." And Nissen reportedly observed in Norway a lack of significant correlation between collection locality and a number of morphological characteristics.

To further examine this flexibility, sods of natural Kentucky bluegrass in 6-inch squares were gathered from many marked locations and assembled in central Ohio. These, of course, are not truly clones, but clone-like do perpetuate a given sod complement. A number of the collection sites were visited several times, most of them at least once in autumn and several springs. It is difficult to make meaningful

[1] Only occasionally was there hint of better performance from local strains rather than from distant ones, this towards the margins of what could be considered good bluegrass country. Comparative performance is hard to measure, and if there was any significance it seemed to lie more with debilitation of northern ecotypes moved southward (to latitudes of Tennessee and Missouri), rather than the reverse.

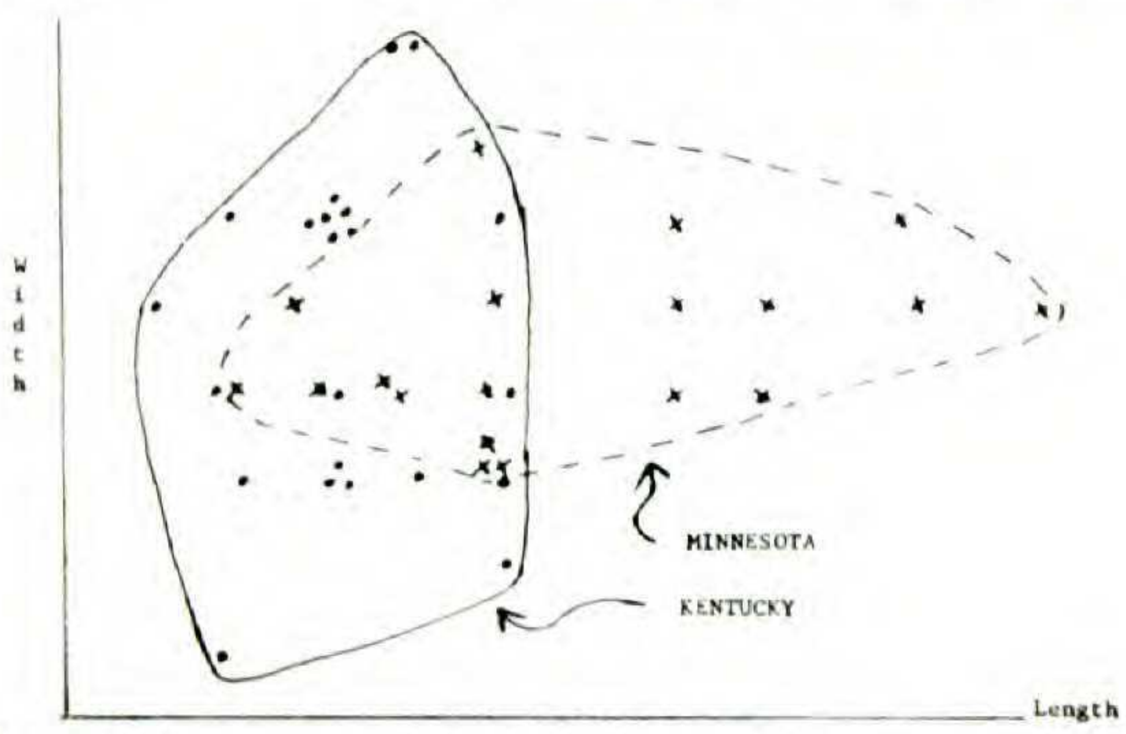

CHART 1—Comparison of the number 1 (tip) leaf on non-flowering culms of Kentucky bluegrass, in Kentucky as contrasted with Minnesota. The more extreme (longer leaf) measurements for Minnesota are those from the northern part of the state; those nearer like Kentucky are from the southern part.

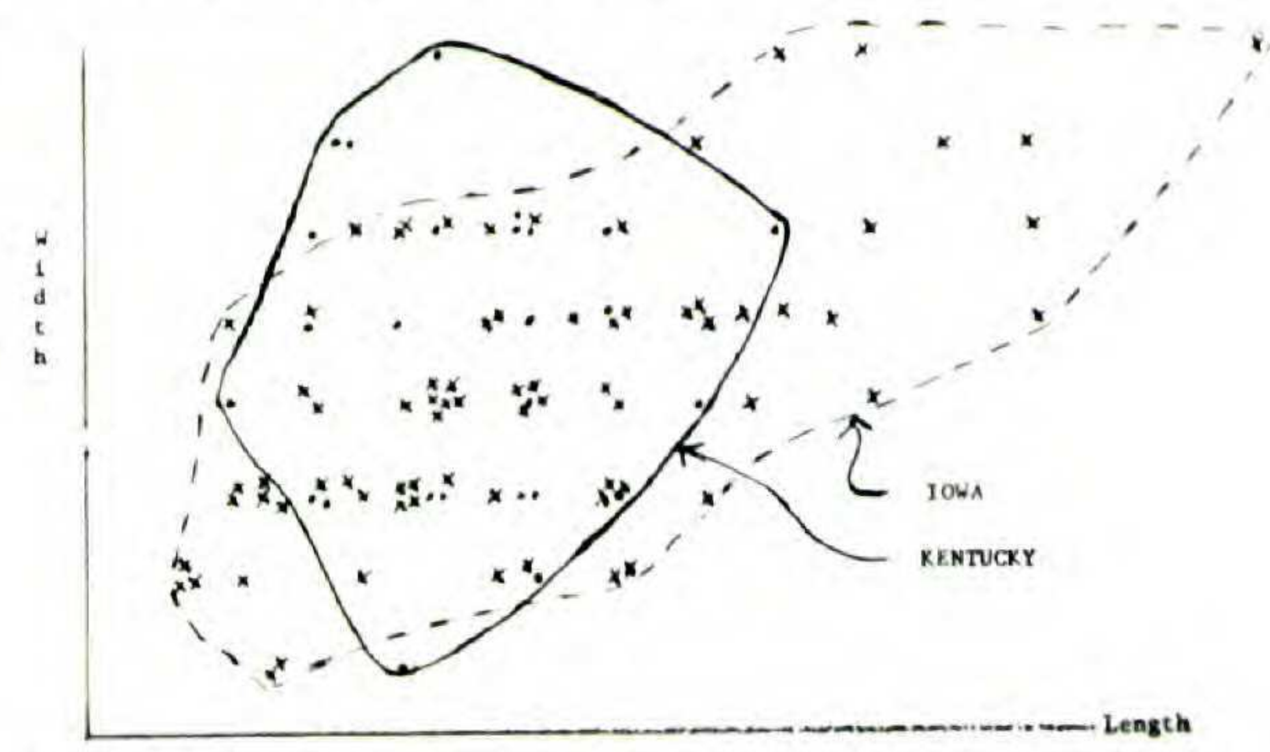

CHART 2—Comparisons of the number 2 leaf (second from tip) of non-flowering culms of Kentucky bluegrass, from Kentucky and Iowa. There's a great deal of overlap, but a tendency in Iowa for leaves to become longer, and then show less variability in width.

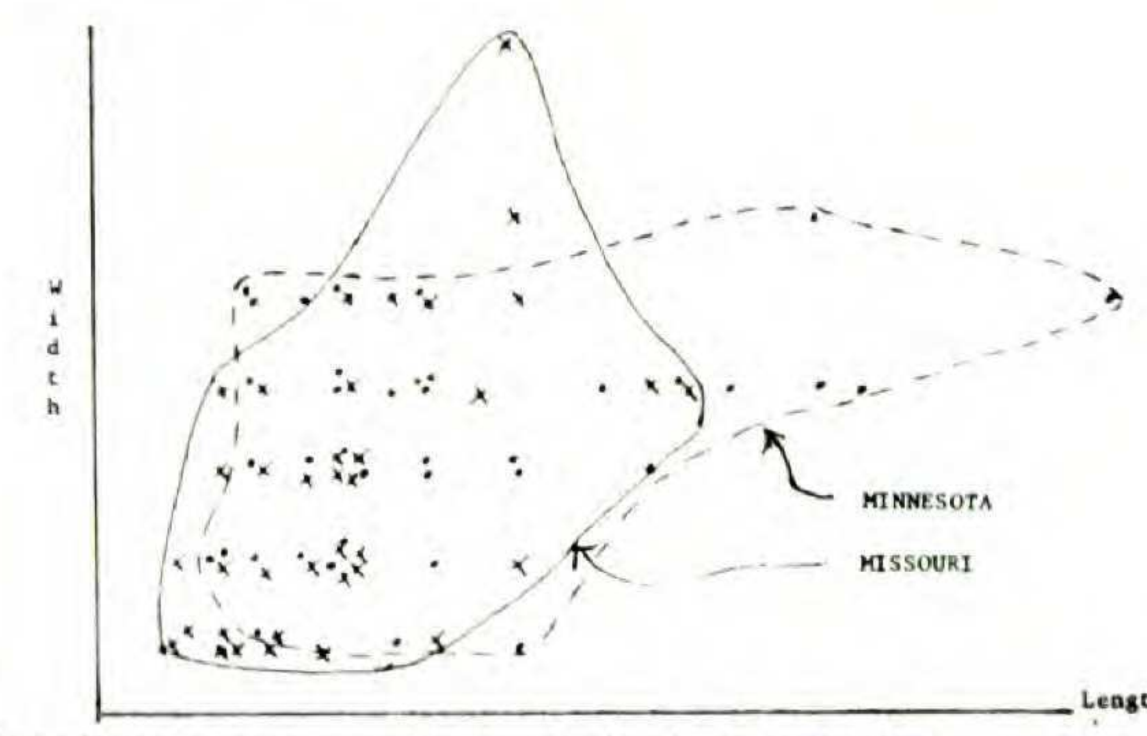

CHART 3—Comparison of leaf 3 (third from tip), on non-flowering culms, of Kentucky bluegrass from Missouri and Minnesota. The width/length spread for Missouri is not a whole lot unlike that noted for Kentucky in previous charts, and seems to differ from more northerly populations in the same general way (if not to the extent) that was the case when comparing Kentucky grass (Chart 1).

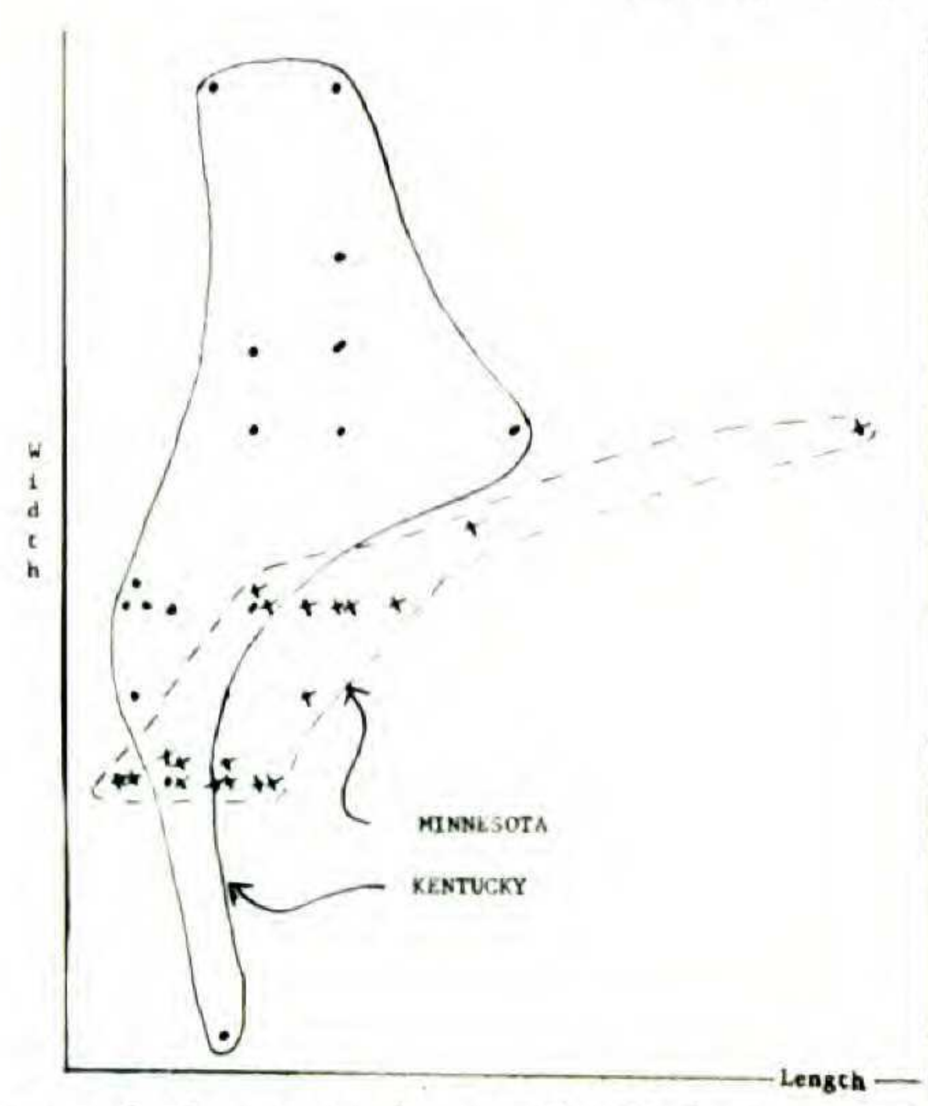

CHART 4—Comparison of the second panicle leaf, on Kentucky bluegrass from Kentucky and from Minnesota. Again, the extremes in length for Minnesota are from the northern part of the state (viz. Chart 1).

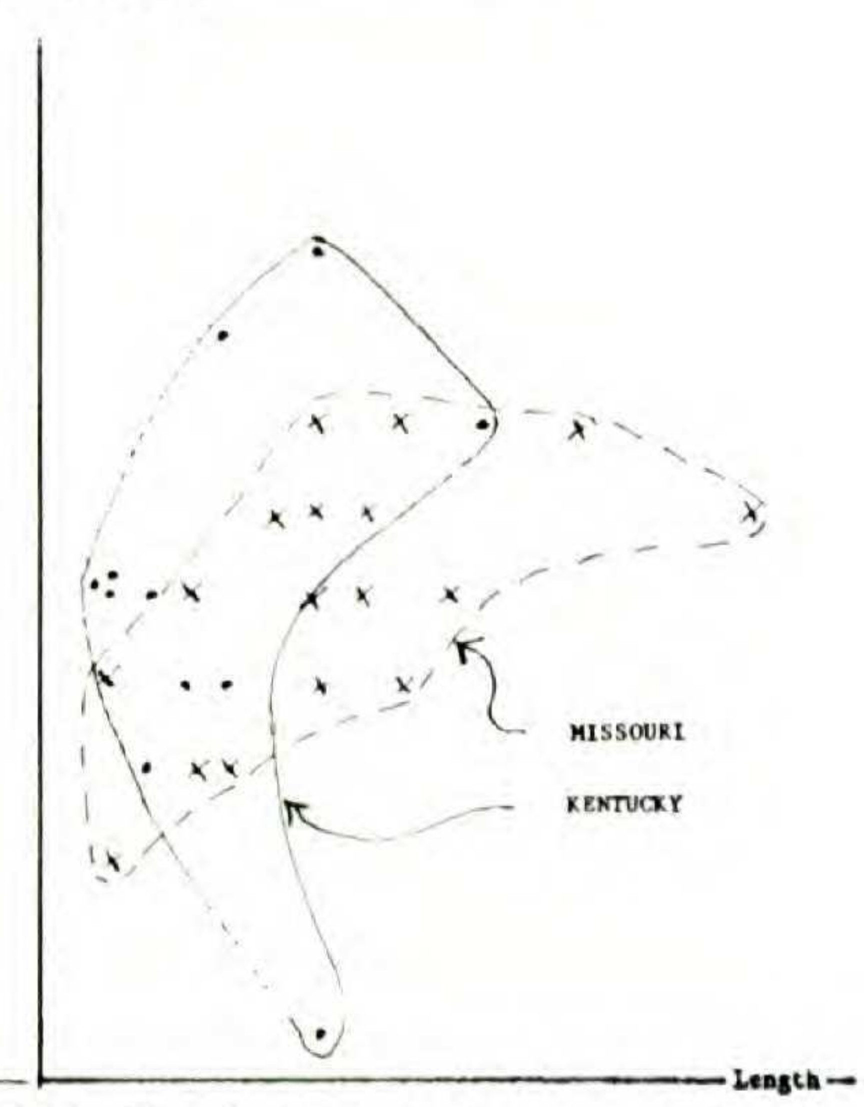

CHART 5—Comparison of the second panicle leaf of Kentucky bluegrass from Kentucky and from Missouri. It appears that the trend manifest for Minnesota in Chart 4, is already indicated in Missouri.

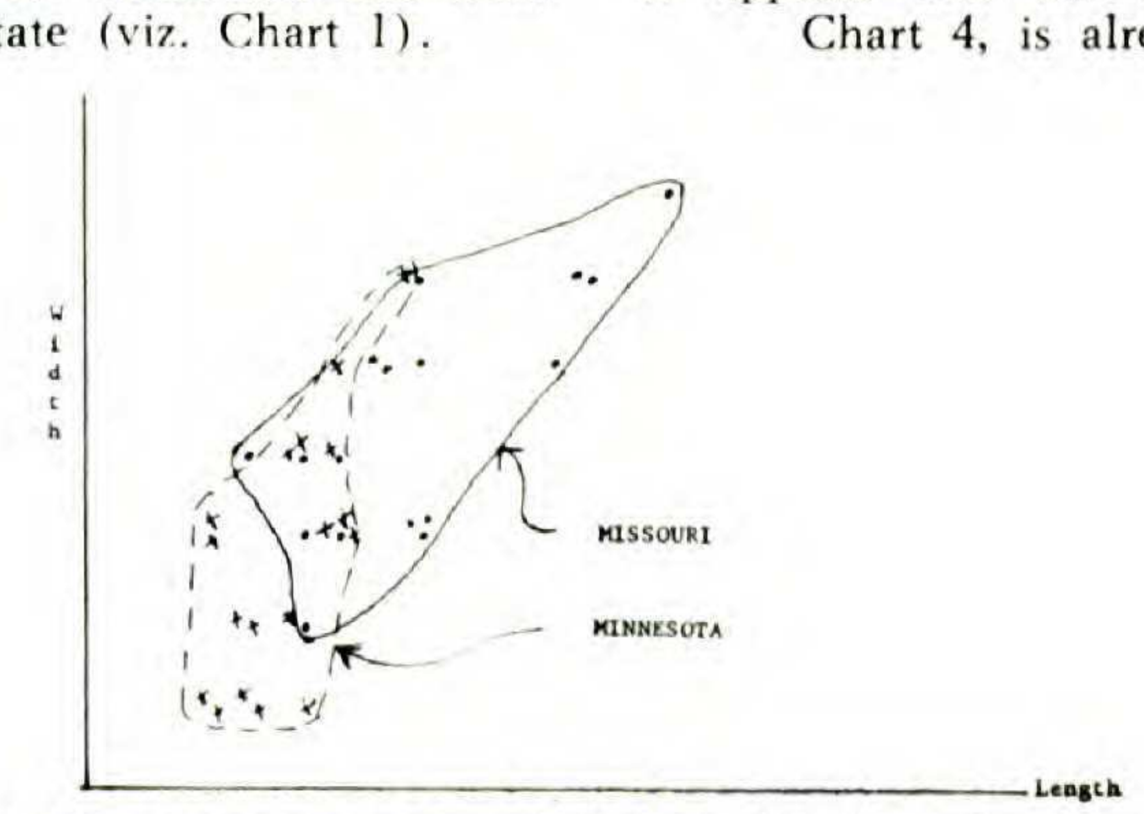

CHART 6—Comparison of the tip (flag) leaf on young panicles of Kentucky bluegrass from Missouri and Minnesota. Although Minnesota flags average shorter, there is perhaps greater genetic restriction.

phenotypic records of a heterogeneous population, so a simple leaf width measurement was settled upon, one of the characteristics used by Bär (7) and others in comparison.

Data was reported to the Botanical Society at the AIBS meetings at Stanford University in 1957, under the title of "The Remarkable Plasticity of Bluegrass *(Poa pratensis)*." Because of practical difficulties in assembling numerous sods from distant areas, because human judgment is not precise in selecting comparable leaves for measurement (equivalent stage of maturity), and because the measurements were made fairly grossly with a ruler, no claim is made for statistical significance in the figures. Nevertheless, Tables 1-4 do suggest average populational differences. Likewise, scatter-diagrams, samples of which are included as Charts 1-6, suggest a broader and somewhat differing gene pool in certain locations as compared to others. Kentucky, probably an early center for dispersal of bluegrass into the Midwest and northward, seems to have its bluegrass more diversified than the newer bluegrass populations that have colonized northern fields more recently (viz. Minnesota; upon abandonment from cultivation after World War II). This conclusion fits nicely the Vavilovian concept of dispersal of more restricted genotypes from a variable center of origin.

Regional differences in the field are often dramatic. The tussock habit of Kentucky bluegrass north and west from approximately Aberdeen, South Dakota is notable. There, and on some of the sandy soils of old Lake Agassiz (Red River Valley, North Dakota) the grass is highly untypical of that in the lower Midwest. The plants are widely spaced, in discrete clumps, rough and siliceous to the touch, unusally erect (not tending to spread and flop), the leaf margins often inrolled (looking more like a fine fescue than a bluegrass). Panicles are compact, and as seed harvesters well know, seed from northerly regions tends to be heavier and less chaffy than that in the South. Yet such sod planted in Ohio turns almost indistinguishable from Ohio sod! The uncommon field appearance must in large measure be adaptation of a flexible genetic base to the local environment—perhaps harsher, more desiccating; the soil more nearly virgin, undepleted; with meadowing practiced on northern grass, pasturing on southern; etc.

Such differences in the field can be verified simply by shoot counts. The number of culms per square foot of sod (late September and early October) averaged about 630 for Kentucky-Missouri-Iowa, only 440 for South Dakota—North Dakota —Minnesota (based upon scores of samplings). In spring a series of sods in Kentucky averaged about 1200 shoots per square foot, while in South Dakota (at an

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CHARTS 1-6. Scatter-diagrams comparing width/leaf measurements for equivalent leaves on both flowering and non-flowering culms, for the states indicated on the individual charts. Other leaves, and other state comparisons, fall generally within the trend noted in these six examples. The variable width and comparatively modest leaf length exhibited by Kentucky populations, trends gradually to restriction in width and greater length, westward and northward into Missouri, Iowa and Minnesota. This is essentially the progression of settlement, and it may be that especially adaptive genotypes (for prairie conditions) moved from an original center near the Ohio valley into newly cultivated lands northwest. The progression is still moving westward, with Kentucky bluegrass showing up in western Nebraska, Wyoming, and other areas where none was known some years ago.

estimated equivalent stage of development) the count was only 680, in Minnesota 570, and in North Dakota 470. Obviously, density peters out northwestward, for whatever the cause.

But as Rollins (8) points out, one of the first tasks in study of a species is to find out which part of the phenotypic variation is correlated with environment, and which part is under direct genetical control. That not a great deal of this density difference is genetic, can be shown by comparison of populations receiving differing treatment in a given area. For example, in Missouri and Iowa, spring shoot count for heavily grazed pastures reached 1330, while nearby ungrazed fence rows had a shoot count of only 544. On the grazed areas there were many more shoots and leaves, but these were quite dwarfed. While I am confident that there is more bluegrass (of greater diversity) per square foot in Kentucky than in North Dakota, I do think the earlier shoot count figures are misleading chiefly because Kentucky grass is mostly grazed, Dakota grass cut for hay. We know in lawn tending that management generally overshadows varietal choice!

Let us turn to the scatter-diagrams Charts 1-6. These match leaf length against width, on a series of regional sods, taken dormant, then forced in the greenhouse. Measurements were made at early inflorescence. Both vegetative and fruiting culms were compared, with reasonable care taken to choose leaves of equivalent maturity. While there is much overlapping and variability, a general trend appears to exist. Using Kentucky grass as the base for comparison, leaves tend to be longer and less variably wide westward and northwestward, at least in younger foliage. There seems to be greater variability (a larger gene pool?) in Kentucky and in the South, than with newer populations farther north!

Mean differences in leaf width are given in Table 1. Here too, there is generally less variability, narrower leaves, in the North than in the South.

But in Table 2 we see the beginnings of conformity to a new environment. Sods of Table 1 (planted out) had leaf width measured in July, three months after the Table 1 recordings. There is some convergence.

Table 3 gives mean leaf widths the next following growing season. Here the spread is narrowed further (although the sods are not exactly those of Table 2).

Table 3. Mean leaf width of sods 2nd year after planting out. Figures in 1/32nds of inch, based on 200 leaf measurements, given in 1/32nds of inch.

Source	*mean leaf width* *July*
South (Kentucky)	3.12
South (Missouri—Iowa)	3.02
North (lower Minnesota—Dakotas)	2.96
North (upper Minnesota—Dakotas)	2.84

Table 4 compares populations (sod) started from seed from known locations. There is no logical explanation why South Dakota and North Dakota should seem so untypically different from one another, other than to point out again that what part of a harvest ends up as an individual seed lot may have a greater bearing than does region of production.

To summarize, I excerpt the abstract from my Golden Jubilee Agronomy meet-

Table 4. Inflorescence and leaf measurements of unmowed row plantings in 2nd year, from known-origin seed. Seed fractionation and measurements showed no correlation. In mm.

	mean infloresc. length	*range*	*samples*	*mean width 2nd panicle leaf*	*range*	*samples*	*mean veg. leaf width*	*range*	*samples*	*"widest" leaf mean of 3*
N. Dak.	85	(55-125)	84	3.9	(3.0-4.9)	51	2.3	(1.7-3.2)	90	5.0
S. Dak.	74	(45-100)	69	3.1	(1.9-4.5)	43	2.0	(1.2-2.8)	73	5.0
Iowa	81	(45-110)	88	3.7	(2.4-5.2)	48	2.3	(1.2-3.5)	81	5.4
Nebr.	99	(50-170)	96	3.8	(2.2-5.5)	59	2.3	(1.7-3.5)	89	6.2
Ill.	86	(65-110)	20	3.9	(2.9-5.2)	20	2.3	(1.4-3.0)	37	4.6
Ky.	86	(55-120)	44	4.2	(3.0-6.2)	25	2.5	(1.2-5.0)	74	6.3

ings paper, "Regional Adaptation in Kentucky Bluegrass:" "Compared to corn, wheat, alfalfa, and familiar crops having strains adapted to limited climatic zones, Kentucky bluegrass perhaps presents a unique example of widespread adaptability and plasticity. Phenotypic adaptation suggests an extremely flexible genotype. Kentucky bluegrass selections from as far north as Canada to as far south as Missouri and Kentucky, survive well side by side when planted in multiple environments throughout the northern two-thirds of the country. Although more diversity is evident in southern areas, the very different appearances in field and meadow is more an adaptation to soils, rainfall, and method of use than to stable genetic qualities.—" The Kentucky bluegrass phenotype appears quite laxly under genetic control.

This broad flexibility noted in *Poa pratensis* is not typical of most plants. Hanson & Carnahan (9) indicate that though cool-season grasses are usually widely adaptable, seldom are range species suitable for zones greater than 300 miles in latitude. McMillan (10) notes ecotypic differentiation in prairie grasses persisting within transplanted community fractions, with a rigidity Kentucky bluegrass does not display. In controlled climate chambers there was a deleterious sensitivity to changed environment that natural bluegrass seems unbothered by. Peacock & McMillan (11) pinpoint regional adaptation of physiological nature in mesquite, relating to photoperiod, temperature, onset of dormancy, resistance to freezing, and so on,—adaptations certainly not very fixed in natural Kentucky bluegrass.

Kentucky bluegrass' genetic "mix" evidently allows the grass a terrific range of response. This has enabled it to follow man the world around and become a dominant wherever good soil is turned. How like the world's most successful "weeds," as characterized by Harlan & de Wet (12): "Most weeds are characterized by enormous phenotypic plasticity. Under favorable conditions, a given genotype may be tall, robust, well developed and highly productive. Under unfavorable conditions, the same genotype may be minute, depauperate, living but a short time and producing only a few seeds." With wild oats, Harlan observes: "The nursery contained winter forms (of crop) which were still in winter rosette when spring forms in the same field were tall and heading out and some of the earliest varieties maturing. In the barley, these differences in growth habit were genetically controlled. But the wild oats with which the field was infested produced phenotypic mimics of all the growth habits. When growing with winter barley, the wild oat formed a low winter rosette; in adjacent rows of spring barley, the wild oats were tall and heading out. Where the early barley was maturing, the wild oats were ripening. All stages could be seen on the same day. The capacity for phenotypic mimicry is presumably under genetic control and constitutes an excellent adaptive mechanism."

Although Kentucky bluegrass is certainly well adapted in the modern (disturbed) world, one wonders how well it might have fared in pre-historic American grassland communities had it then been in the New World? As to what causes the American grasslands, Wells (13) hypothesizes on paleobotanical grounds that the grassland provinces of central North America are relatively recent, correlated with young (Pleistocene) transported soils, flattish terrain; these features interacting with wind and fire to maintain the grassland. Nothing insurmountable here for bluegrass! Iltis (personal communication) is convinced that periodic burning is needed to retain native prairie in Wisconsin, in competition with "more aggressive" *Poa pratensis* and *Poa canadensis.* I expect, that in spite of occasional fire and desiccation, a species with such versatility as *Poa pratensis* shows, would have maintained a primeval foothold. I've seen it take hold in isolated montane valleys of southwestern Colorado, where the sole disturbance has been grazing (and trampling) by occasional roving livestock.

Kentucky bluegrass constitutes one of the world's most abundant and useful species, much studied, yet still enigmatic. How do variable chromosome number, facultative apomixis and similar attributes relate to the great success of Kentucky bluegrass? What were the ancestral diploids like, and where native? How can special traits be selected for, yet preserve the invaluable adaptability of natural Kentucky bluegrass? Useful genotypes, such as Merion and a few other cultivars, can be maintained under reasonably accurate identity by roguing the relatively infrequent sexual off-types and mutants. But such useful finds are seldom the equal of natural Kentucky bluegrass in self-sufficiency over the tremendous range that bluegrass occupies.

In any event, the ability of Kentucky bluegrass to mold easily and quickly to changed enviorment augurs well for its continued ubiquity and importance. With monoculture and "identicalness" the order of the day, versatile Kentucky bluegrass, proven to have the stuff for survival to an extent exhibited by few Spermatophytes, may have much yet to offer, practically, esthetically and as a source for additional genetic information.

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